THE SCHIZAEACEAE OF THE SOUTH OF ENGLAND IN EARLY TERTIARY TIMES

By M. E. J. CHANDLER

SYNOPSIS

The paper records the discovery of two new species of *Anemia*, *A. poolensis* and *A. colwellensis*, and one of *Lygodium*, *L. poolensis*, in the early Tertiary strata of Britain. It also gives new information about *Lygodium kaulfussi* Heer from fertile material. Fertile pinnules of all these species are so beautifully preserved that more is now known in detail of some of these fossils than of many living species. Previous knowledge of British Tertiary Schizaeaceae is summarized. Fuller and more satisfactory evidence that the two genera once grew in southern England supports other evidence from fruits and seeds (awaiting publication) of a very warm and humid climate in the south of England throughout the early Tertiary period.

INTRODUCTION

Previous knowledge of the Schizaeaceae in the English Tertiary was based on sterile fronds of *Anemia subcretacea* (Sap.), *Lygodium prestwichii* Gard. & Ett. and *Lygodium kaulfussi* Hr. together with some imperfectly studied fertile fragments of the last species. Like the contemporary angiosperms these ferns indicate a very warm and humid climate. They are perhaps survivors of an ancient widespread more or less uniform broad Mesozoic tropical belt of vegetation. For *Anemia* appears to be a relict genus in the old world, where it is now represented by few species although the genus was formerly widespread. But it flourishes and is represented by numerous species in the tropics and subtropics of the New World, albeit with a restricted northern range. *Lygodium* still holds its own in both hemispheres with a shrunken latitudinal area of distribution which can be attributed to the universal post-Eocene cooling of climate and consequent contraction of the tropical and subtropical belt of vegetation.

This paper is a bye-product of research upon the fruits and seeds of Tertiary Beds in Dorset, Hampshire, and the Isle of Wight. The material first to be described was found in abundance while sifting carbonaceous sands in the Lower Bagshot Beds (Cuisian ?) on the north shores of Poole Harbour at Lake, near Hamworthy, Dorset. The matrix was coarse and rich in seams of wood and fruits among which were small, often crushed and contorted, ovoid or subglobular, segmented bodies. The majority had tightly enrolled segments of distinctive appearance. When moistened with alcohol or nitric acid on a glass slide and examined under the microscope, quantities of large globular-tetrahedral spores were released among which were many larger turgid bolster-shaped or fusiform objects of spore-like appearance.

Further investigation showed that on the inner surface of the enrolled segments sporangia were seated apparently in two rows. They had the typical apical annulus of Schizaeaceae, but the occurrence of what appeared to be two types of spore presented a problem for which botanists who were consulted could produce no ready solution.

In due course the specimens were shown to the late W. N. Croft. With characteristic generosity and interest he gave up many hours to the investigation of the matter, studying with painstaking thoroughness not only the evidence yielded by the fossils, but all that could be discovered from living material of *Anemia.* In addition he searched the literature of Recent ferns, and such published work as is available on fossil Schizaeaceae in the hope of obtaining a clue to the mystery of the two types of "spore". As the result of a very large amount of work Mr. Croft discovered that the turgid elongate "spores" were really paraphyses such as are found growing among the sporangia on the surface of Recent fertile *Anemia* pinnules. The relationship of the fossils to *Anemia* was then demonstrated by cell-structure, sporangia and spore-characters and a spore-count. Mr. Croft was also responsible for most of the fine series of highly magnified photographs of sporangia, spores and paraphyses shown in the accompanying plates.

It was our original intention to produce a joint paper on this species, here named *A. poolensis.* But unfortunately Mr. Croft died before the work was finished. It therefore remains for me to record the results of our efforts and to pay tribute to the work of a most generous and able colleague. It can be claimed that more is known of the fruiting organs of the fossil species *A. poolensis* than of many of the living species of this large tropical and subtropical genus. The same species was found represented by one pinnule in somewhat younger beds at Sandbanks and at Branksome Dene in the Bournemouth Freshwater Beds (Lutetian ?) where several macerated pinnules occurred. It was represented at Cliff End near Mudeford (Auversian ?) by a minute fragment which yielded spores, and by a solitary spore at Alum Bay, Isle of Wight (Lower Bagshot, just above the pipe clay) where, according to Gardner & Ettingshausen (1880 : 47), Heer was confident he had seen a barren pinnule of *A. subcretacea.*

While working on *A. poolensis,* I had the good fortune to discover a tiny fertile pinnule of a second species of *Anemia* in the Upper Headon Beds of Colwell Bay, Isle of Wight. It is here described as *A. colwellensis.* In spite of prolonged search and sifting no second specimen has yet been found. It occurred in a small pocket of broken and battered fragments which included scraps of *Gleichenia.*

A second genus of Schizaeaceae, *Lygodium,* represented by fruiting pinnules of two species also turned up at about the same time. One was closely associated with barren pinnules of *L. kaulfussi* at Studland (Cuisian ?) and may be presumed to belong to that species. It was also found in the Bournemouth Freshwater Beds at Branksome Dene, Dorset. The species formerly occurred in considerable abundance at Bournemouth, chiefly as barren pinnules but rarely as fertile ones. The other was represented by a naturally macerated fertile pinnule in fine sediment at the base of the section at Lake. Its spores demonstrated beyond question that it is specifically distinct from *L. kaulfussi.* It has been named *Lygodium poolensis.* A solitary spore was subsequently recognized entrapped among the hairs of *Anemia* on slide V.31511.

The importance of these discoveries lies in the fact that hitherto the occurrence of Schizaeaceae in the south of England has been based on barren pinnules only, if we except the imperfectly investigated fertile tufts of *Lygodium* figured by Gardner & Ettingshausen from Bournemouth (see below). The fertile fragments hereafter described confirm the earlier work by providing fuller and more satisfactory evidence that the genera *Anemia* and *Lygodium* once grew in southern England. The presence of this essentially tropical family supports evidence from fruits and seeds (awaiting publication) of a very warm and humid climate in the south of England throughout the earlier Tertiary period.

Previous work takes account of three species only : *Anemia subcretacea* (Saporta) from the Bournemouth Freshwater Beds and Reading Beds, *Lygodium prestwichii* Gard. & Ett. from the Woolwich and Reading Beds, and *Lygodium kaulfussi* Heer from the Bournemouth and Studland Beds. A brief account of these three species as recorded in literature is given here, while *L. prestwichii* is also described from a new site at Newington, Kent and *L. kaulfussi* from fresh barren material from Studland as well as from the newly discovered fertile material. A few barren pinnules from the Bembridge Beds originally described as *Filix incertae sedis*, sp. 5, can now be referred with reasonable certainty to a species of *Anemia* although few of its characters are known. Its nervation and pinnule margins are strongly reminiscent of the fertile pinnule segments of *A. colwellensis*. As there is no definite connecting link between the two, however, the Bembridge pinnules must be regarded, for the time being at least, as representing a third species.

Genus *ANEMIA* Swartz

NOTE : The spelling of the generic name is that given in the code of Botanical Nomenclature 1952, p. 83.

Anemia subcretacea (Saporta)

1868. *Asplenium subcretaceum* Saporta, p. 315, pl. 23, fig. 4.
1880. *Anemia subcretacea* (Saporta) Gardner & Ettingshausen, p. 45, pls. 8, 9.
1882. *Anemia subcretacea* (Saporta) : Gardner & Ettinghausen, p. 67.
1886. *Anemia subcretacea* (Saporta) : Gardner, pp. 400, 402, pl. 1.

The fern is illustrated and fully described by Gardner & Ettingshausen (1880) from the Bournemouth Freshwater Beds, and is illustrated by Gardner (1886), but without full description, from the Reading Beds of Reading.

The specimens are preserved in the British Museum (Natural History) Geology Dept., Nos. V.14970–73 and V.15033–42 (Bournemouth) and V.15272 (Reading).

According to Gardner the barren pinnules were very abundant at Bournemouth especially to the east of Bournemouth pier, decreasing in size and abundance westwards towards Poole Harbour, while at Branksea only small pinnules occurred. He comments that the fertile pinnules, which he had never seen, were almost certainly separate and therefore rarely if ever preserved. He added that although the fern "did not agree very closely with any existing species of *Anemia*, the general form and dichotomy of the frond, the venation, the length and strength of the stipes, the separation of the fertile and barren pinnae, have, after much consideration, induced us to place it in the genus *Anemia*". He compared it with *A. adiantifolia* Sw. from Cuba, the Bahamas, Florida and Mexico to Bahia.

Gardner & Ettingshausen (1880 : 47) report that Saporta, who had evidently compared Bournemouth specimens with similar ferns from Sézanne, had no hesitation in stating that the two were identical, while Lesquereux compared them with some from the Eocene of North America and could see no difference whatsoever. Gardner & Ettingshausen (1882 : 67) add that the species is characteristic of the "older Eocene, and even pre-Eocene Rocks". They state that it first appeared in the Cretaceous and its upper limit in Europe is the Bournemouth horizon and that it attained its greatest luxuriance in the Eocene Beds of what are now temperate latitudes although it ranged from the south of France to the Arctic regions.

This barren foliage closely resembles specimens of *Anemia fremonti* Knowlton and *Anemia* sp. figured by Andrews & Pearsall (1941, pl. 5, figs. 30–32, 34, 35) from the Upper Cretaceous Frontier Formation of south-western Wyoming, U.S.A.

The discovery of abundant fertile pinnules of *Anemia*, described below as *A. poolensis*, in the Bournemouth Beds (Cuisian or Lutetian ?) of the western end of the Bournemouth section raises the question whether these detached fragments are the fertile form of *A. subcretacea*. The relationship cannot be proved in the absence of any organic connection and in the absence of the two forms in close association in the same layers. They are separated therefore for the time being although it is quite possible that future evidence may make it necessary to unite them under one specific name. Should this eventually happen the character of the spores (p. 301, Pl. 33, figs. 24–31 ; Pl. 36, figs. 54–58) would clearly separate *A. subcretacea* from *A. fremonti* forma *fertilis* Andrews and therefore presumably from the barren *A. fremonti* Knowlton. Nevertheless it is interesting that species of *Anemia* with the same type of foliage existed in Cretaceous and Eocene times in the two hemispheres, and that in both the genus extended far to the north of its main present day range in tropical and subtropical latitudes. In America *Anemia* is found only as far north as the Sierra Nevada and Florida but is richly represented by many species in Central and South America and the West Indies, especially in mountainous regions. In the Old World today it survives only as a relict genus with a very few species, one *A. lanipes* Christensen in Madagascar, one *A. schimperiana* Presl. in tropical Africa and South India, and one *A. dregeana* Kze in Natal. The genus may perhaps be regarded as a representative of that ancient more or less uniform tropical plant belt of low latitudes in Cretaceous times. For unknown reasons it persists as a vigorous component of the tropical and subtropical flora of the New World up to the present, but in spite of its former wide range in the old world it remains there now only in an attenuated form although in the equatorial belt the climate was probably always favourable to it. But outside the tropics where colder conditions prevailed after the Eocene it was exterminated altogether.

Anemia poolensis n. sp.

(Pl. 32, figs. 1–10; Pl. 33, figs. 14–22, 24–31; Pl. 34; Pl. 35, fig. 41; P.l 36, figs. 54–58; Text-figs. 1, 2)

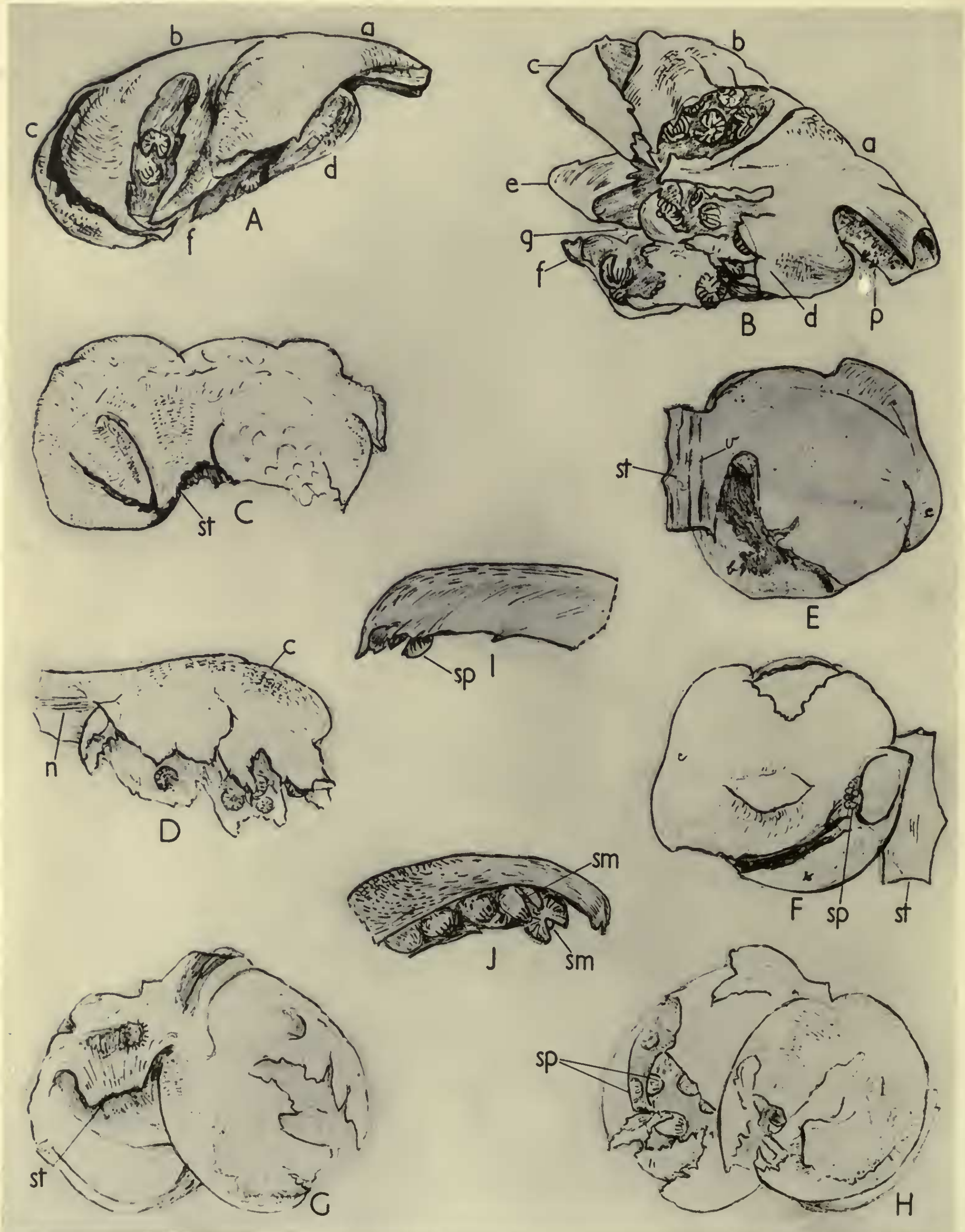
DIAGNOSIS. Fertile pinnules deeply divided into a varying number of segments, 4 to ? 7, some of the segments being further dissected and often somewhat twisted. Segments strongly recurved so as to form a compact body about 2 or 3 mm. across (often open below), foliose, irregularly and deeply toothed or jagged especially distally, often sharply pointed, sometimes boat-shaped, occasionally clothed with a felt of pointed usually non-septate hairs which may occur on both surfaces. Sporangia numerous, sub-ovoid to sub-globular, about 0·25 to 0·44 mm. long and 0·2 to 0·3 mm. broad. Annulus symmetrical, apical, occupying about two-fifths of the length of the sporangium, formed of a single row of about fifteen straight thick-walled cells. Cells of sporangium wall almost straight superficially but when examined with ¼ in. objective having a finely sinuous appearance. Apical plate delicate of about 12–14 cells. Trilete tetrahedral-globose spores entirely smooth, about 50 to 60μ (rarely larger or smaller) in diameter, wall 2 to 2·5μ thick as seen in optical section. Paraphyses many among the sporangia, sessile or shortly stalked, about 72 to 156μ long, 48 to 114μ broad.

HOLOTYPE. V.31484.

DESCRIPTION. *Rhizome and frond* including fertile stipe unknown. Fertile spike probably somewhat flattened in one plane, by inference (see below).

Fertile tertiary pinnae having several segmented pinnules of which one is terminal while the others may spring from one stipe and form a pair of sub-globular bodies (Text-figs. 1 C, G, H) or they may arise singly (Text-figs. 1E, F; 2B).

Fertile pinnules divided sympodially into from 4 to at least 7 segments, some of which may be further dissected and much twisted. Segments strongly recurved so as to form a compact sub-ovoid, sub-globular, or ellipsoid " body " about 2 to 3 mm. across but varying in size with the degree of folding and recurving, largest in the least recurved specimens. Terminal pinnules more simply reflexed than the others in the few such specimens seen, and not enrolled at the distal ends of the segments so that the sporangia on their lower surfaces are partially exposed (Text-figs. 1A, B, D; 2G, H), other pinnules are usually open below to a lesser extent, for not all segments are enrolled distally, so that the " bodies " may gape downwards (Text-figs. 1H; 2A, E, F). Segments rather rigid, foliose, of variable width without indusium-like margins, irregularly and sometimes deeply toothed with sharply pointed narrow teeth and free tips. Hence their distal ends have a jagged appearance (Text-figs. 1A, B, G, H; 2D). These tertiary pinnules (" bodies ") are often somewhat flattened. This appears to have been an original character as indicated by the form of the segments, those which form their lateral margins being frequently folded longitudinally and more or less inverted boat-shaped so that they embrace the adjacent segments (Text-figs. 1 I, J). Those over the middle part of the bodies may be broad or unfolded, they may even be slightly concave outwards with outward curving edges. The boat-shaped lateral segments are unequal sided as a rule, one side of the " boat " being



TEXT-FIGURE 1

TEXT-FIG. 1. *Anemia poolensis* n. sp.

(A) Side view of a terminal pinnule from a fertile tertiary pinna. Stipe to right. Five recurved toothed segments (*a, b, c, d, f,*) are shown with a few sporangia exposed in the gaps between them. Direction of cell-structure indicated on the upper surface of the segment. Length, 3·1 mm. × 20 approx. Holotype V.31484.

(B) Under surface of the same. More of the recurved segments are seen *a, b, c, d, f,* as in A, *e, g,* additional segments not visible in A. Note the sporangia. Paraphyses were attached at *p*. × 20 approx.

(C) A pair of tightly reflexed downwardly directed pinnules (1) and (2) showing the broken end of the stipe (*st*) from which they spring. Length, 2·4 mm.; breadth across the pair, 3·25 mm. Surface much sand-pitted in places. × 17 approx. V.31485.

(D) A terminal loosely recurved pinnule. It was originally united on the left to a stipe which bore two other fertile pinnules (now detached). Length about 2·5 mm.; height, 1·6 mm. (*n*) is a nervule flanked by fragments of reduced fronds. (*c*) Indicates shining cells with digitate walls. Under the microscope the walls appear raised and rounded, the centre of the cells depressed. There are sporangia on the lower surface. × 17 approx. V.31486.

(E) A tightly recurved and enrolled single pinnule still attached to a large fragment (1·4 mm. long) of stipe (*st*) of the tertiary pinna. The midrib of the stipe is channelled on the upper surface at (*v*), the channel marking a vein flanked by reduced lamina. (*b*) and (*c*) are two segments. Maximum diameter at right angles to stipe about 2·75 mm. × 15 approx. V. 31487.

(F) Reverse side of E. (*st*) stipe, (*b, c*) correspond to segments so labelled in E. A mass of spores liberated from a disrupted sporangium is indicated on the right at (*sp*).

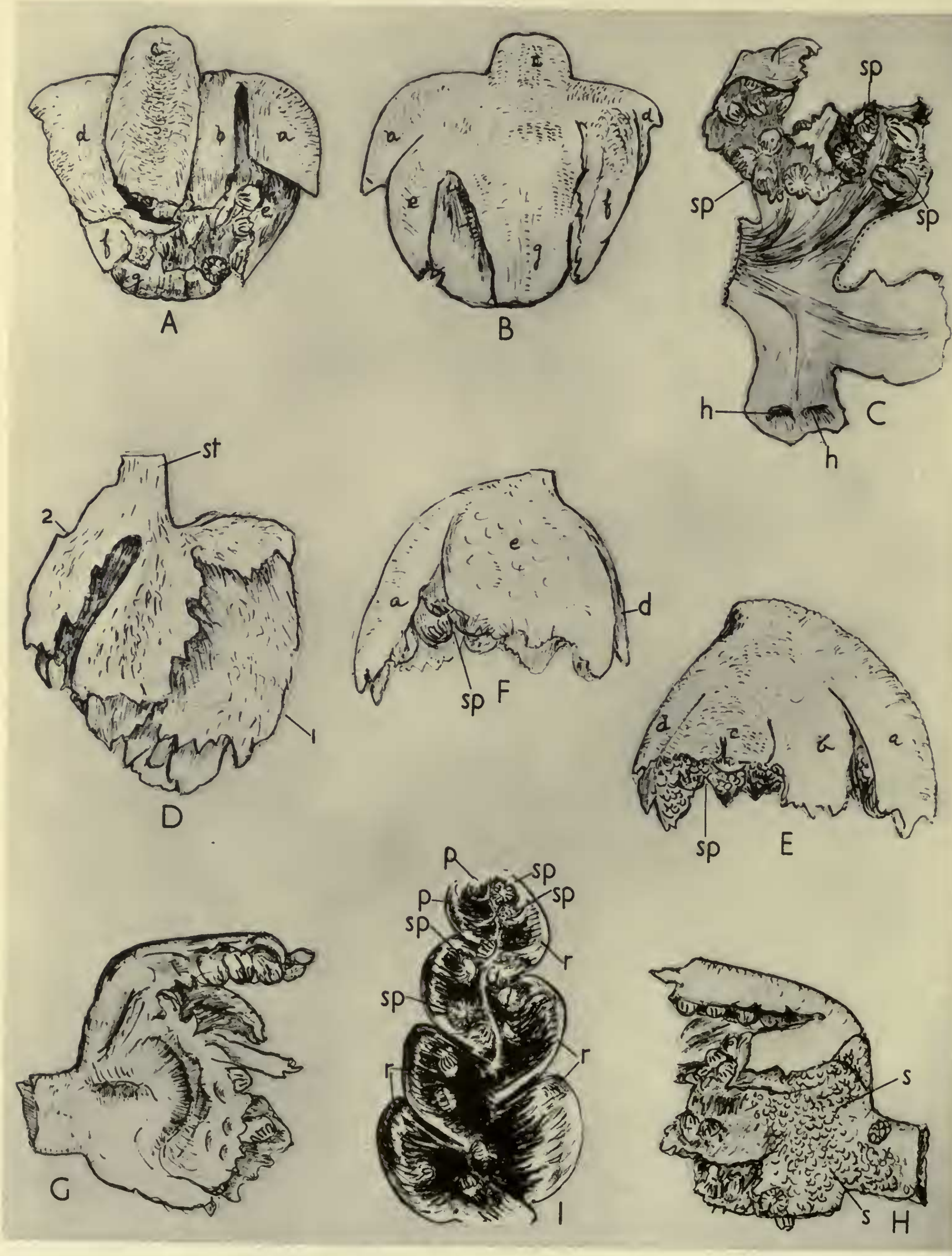
(G) A pair of tightly reflexed downwardly directed pinnules still attached to the remains of a stipe (*st*). Length about 2·75 mm.; across the pair, 3 mm. × 17 approx. V.31488.

(H) Reverse side of the same specimen showing the reflexed segments of the two pinnules, with a few sporangia (*sp*) exposed.

(I) A detached typical unequal-sided boat-shaped segment showing the upper surface. A sporangia projects from below at (*sp*) with open stomium. Oblique striae diverge from the nervule over the surface on this side of the segment. Proximal end to right. Length preserved 1·8 mm.; depth, 0·75 mm. × 20 approx. V.31489.

(J) Opposite side of the same segment which displays more of the under surface owing to the inequality of the sides of the segment. Proximal end to left. Six sporangia are shown, the two at the distal end with gaping stomium (*sm*) directed to the margins of the segment. Orientation of cells indicated on the upper surface. × 20 approx.

All the above are from Lake, nr. Hamworthy, Dorset.



TEXT-FIGURE 2

TEXT-FIG. 2. A–H. *Anemia poolensis* n. sp. I. *Anemia colwellensis* n. sp.

(A) Sharply reflexed pinnule with downwardly directed segments (*a–f*). A few sporangia are exposed where they gape. The direction of the cells, transverse over the middle of the segments, diverging near the edges, is indicated. Length, 2·25 mm.; breadth, 2·5 mm. (*g*) is the lower surface of the stipe. × 20 approx. V.31490.

(B) The reverse of A. Segments and stipe lettered to correspond with A.

(C) Part of an unrolled pinnule, lower surface. Tips of segments at the base of the figure appear to be broken.. The segments above retain their sporangia (*sp*). The segment below shows hollows (*h*) from which sporangia have fallen. The nervules of the segments are indicated where they could be traced. Maximum diameter of the specimen, 2·5 mm. Maximum length preserved measured along the nervule, about 1·5 mm. ×27 approx. V.31491.

(D) A pair of pinnules, one large (1) the other small (2) borne on the stipe (*st*). Segments much folded together. Surface covered with a felt of hairs, indicated only, in the drawing. Length, 3 mm.; breadth, 2·75 mm. This specimen yielded a smooth spore identical in all its characters with those of the smooth hairless specimens (see V.31506). × 17 approx. V.31492.

(E) A pinnule originally more or less complete but now with the tips of the segments broken. Segment lettered (*d*) may be the stipe. Direction of cells indicated on the surface. Sporangia and released spore masses are seen in the opening below. Length, 1·5 mm.; breadth, 1·75 mm. × 24 approx. V.31493.

(F) Opposite side of the above showing segments (*a*) and (*e*) much sand pitted. (*d*) again may be the stipe.

(G) Upper surface probably of a terminal pinnule. Sporangia are seen in profile in the segment at the top of the figure. The stomium opens outwards. Surface much sand pitted. Maximum length from tip of free segment to base of stipe (?), 2·5 mm.; breadth, 1·75 mm. × 24 approx. V. 31494.

(H) Opposite side of specimen showing the lower surface of the pinnule with a few folded and twisted segments. Sporangia are seen, but over most of this surface they have been disrupted so that the surface is concealed by a mass of released spores (*s*). × 24 approx.

(I) Lower surface of a fertile pinnule (the only specimen) which yielded all sporangia and spores figured (based on a drawing made before the specimen collapsed). It shows alternating, smooth-edged, rounded segments on opposite sides of the nerve or midrib, their recurved margins (*r*, *r*) which produce the smooth outlines form a fringe-like indusium covering part of the lobes on this surface. The sinuous midrib, and the pocket-like depressions (*p*, *p*) from which sporangia have fallen can be seen. The arrangement of sporangia (*sp*, *sp*) in the lobes on each side of the midrib is indicated. × 20 approx. Holotype. V.31522. Colwell Bay, Isle of Wight.

Figs. A–D, G, H are from Lake, Dorset. Figs. E, F from Sandbanks, Dorset.

considerably broader than the other (Text-figs. 1 I, J). The flattening of the tertiary pinnules suggests that the fertile spike had a tendency to be flattened in one plane in life, but the character seems not to have been constant.

Both surfaces are sometimes clothed with a close felt of red or black pointed usually single-celled hairs (Pl. 32, fig. 6; Text-fig. 2D) pitted or corroded in fossilization. In the majority of specimens seen, these have disappeared, if they were ever present, and a highly characteristic glistening outer (upper) surface is exposed. This is formed of transversely elongate cells over the median longitudinal part of each segment, the cells being also aligned in longitudinal rows. As seen by reflected light they are rather coarse with sinuous outlines having sunk centres and raised margins so that they produce a conspicuous and highly characteristic pattern. In section (Pl. 34, figs. 32, 34, 37) more than one layer of these cells is seen and they appear thin-walled. Towards the edges of the segments the coarse cells give place to finer narrow elongate ones which form oblique striae diverging from the median band of shining cells. Inner or lower surface of the pinnule with similar narrow cells which diverge obliquely from the median line or venule of each segment towards its margins. Venules with ? scalariform thickening (Pl. 34, fig. 36). Granules like chloroplasts are common in many of the cells and also amongst macerated spores. They may occur singly or in groups (Pl. 32, fig. 10; Pl. 34, figs. 37, 38; Pl. 35, fig. 41) and appear sometimes to be aggregated into small irregularly shaped plates in which the boundaries between the grains are more or less obscure. The grains are usually rounded or oval but sometimes subangular. Their average size is about 2·5 to 3·5μ. Similar granules occur in living *Anemia*, e.g. in *A. phyllitides* (L.) where they are greenish and about 3·5μ in diameter but they may be as large as 6μ. In form and occurrence they are like those of the fossil.

Paraphyses (inflated short sterile filaments) (Pl. 33, figs. 18–22; Pl. 34, fig. 37) are abundant all over the lower surface of the pinnules growing amongst the sporangia. They are sub-ovoid to ellipsoid, usually straight, rarely slightly curved, sometimes with a fairly prominent point at the distal end, and a very short stalk at the proximal end. Sometimes they are asymmetrically attached. A few may be sessile. When freshly released from the pinnule segments and scarcely macerated they are shining and turgid, and dark brown in colour. On maceration they quickly collapse, the brown layer within cracks and tends to disintegrate revealing that the paraphysis wall is extremely thin in optical section. The size varies from about 72 by 48μ to 156 by 78μ or they may be as broad and short as 114 by 114μ.

The *Sporangia* (Pl. 32, figs. 4, 5, 7–10; Pl. 33, figs. 14–17; Pl. 34, figs. 33–35, 37; Pl. 35, fig. 41) are shortly stalked (? sometimes sessile) borne in two rows which are closely spaced, alternating and forwardly directed. They arise from the venule or from points close beside it (Pl. 32, fig. 4). In the inverted boat-shaped lateral pinnule segments they project conspicuously above the narrow side of the segment (Text-fig. 1J). They are sub-ovoid, rather broad at the base, attached asymmetrically (Pl. 32, figs. 7, 8). The annulus is apical, symmetrical, well-developed and conspicuous, consisting of a single row of about 15 straight-sided cells (excluding the stomium) the internal and radial walls being strongly thickened. Length of annulus about two-fifths of the length of the sporangium (Pl. 32, figs. 4, 5, 7–10: Pl. 33, figs. 14–17). The stomium consists of two to three rows of cells, dehiscence is longitudinal extending the whole length of the sporangium, normally occurring on the face towards the outer side of the segments (Pl. 32, fig. 5 ; Pl. 33, figs. 14, 15 ; Text-fig. 1J). Apical plate small and circular, very delicate, its distal face with about 12–14 cells, those nearest the centre of the plate equiaxial, five or six-sided with straight sides, those near the edge of the plate broader in a tangential than in a radial direction (Pl. 33, figs. 15, 17). The cells of the sporangial wall appear straight superficially with a 1-in. or $\frac{1}{2}$-in. lens, sometimes they are rounded, at other times pointed at their extremities, elongate parallel to the major axis of the sporangium. When seen from the interior or examined with a $\frac{1}{4}$-in. lens they show a bead-like thickening (Pl. 32, fig. 8) which produces the effect of fine sinuosities on the external surface. Spore output probably 128 (115 actually counted). Length of sporangium about 0·25 to 0·44 mm., breadth about 0·2 to 0·3 mm.

Spores (Pl. 33, figs. 24–31 ; Pl. 36, figs. 54–58) trilete, tetrahedral-globose, non-striate, smooth, glistening, normally about 50 to 60μ in diameter but occasionally as small as 36μ and as large as 70·4μ ; about 2 to 2·5 μ thick, splitting occasionally along the triradiate mark, the distal ends of which sometimes show a fine forking in unsplit specimens (Pl. 33, fig. 27 ; Pl. 36, fig. 54).

REMARKS. These curiously rolled fertile pinnules were chiefly found in the coarser carbonaceous seams at Lake. Numerous specimens have so far been collected and many more would reward persistent collecting and sifting. More than sixty are available for study by reflected light and will be catalogued in a forthcoming British Museum monograph. Many others have been macerated to varying degrees and mounted on slides for examination by transmitted light.

The arrangement of the segments was at first very difficult to discover, but once seen it could be detected almost invariably especially after microscopic examination. In order the better to show structures which are even more obscure in the photographs than in the specimens themselves, sketches have been made (Text-figs. 1 and 2) which are essential to the understanding of these confusing specimens.

The technique adopted in the study of the material was as follows : they were at first examined as a whole by reflected light, a method which best showed the form and alignment of the surface cells, and the arrangement of sporangia and paraphyses on the segments. Many specimens or segments of pinnules were then macerated in nitric acid and mounted, some in xylol, others in Euparal or Canada balsam. They were then examined by transmitted light, and in the case of the denser specimens by strong reflected light using a white background. In this way some of the most delicate structures were seen and photographed. The apical plates of the sporangia were most difficult to display as their delicate cells were peculiarly liable to collapse and tear on maceration. They were most easily seen when mounted in glycerine ; when transferred to alcohol they were frequently disrupted.

Spores and paraphyses were readily released from the sporangia or pinnule segments on moistening with alcohol or nitric acid. The spores were tough and resistant but the paraphyses were so thin-walled that they frequently collapsed as described on p. 300.

A series of microtome sections were prepared under the direction of W. N. Croft.

His notes show that they were cut by Mr. S. Prudhoe from a specimen which was thereby destroyed ; it is now represented by slides V.31506–07, V.31509–10. The " body " was impregnated with paraffin wax after treatment with hydrofluoric acid by the method described by Lang (1929 : 667–8). A first series of microtome sections cut at 10μ (slide V.31507) produced rather incoherent sections and the specimen was re-embedded. A second series was cut at 6μ (slide V.31510). Although less incoherent it was re-embedded. A third series was cut at 10μ (slide V.31509). It held together fairly well but the centre came away as loose powder, due, it was thought to the toughness of some of the tissues. The remaining piece was softened by treatment with tribasic sodium. The fourth series (slide V.31506) was cut from the softened tissue but it appeared to be little better. It was spoilt by the cover-slip sliding over the sections during cleaning. Some of the sections are illustrated in Pl. 34, figs. 32–38.

Fertile pinnules of Recent *Anemia* vary considerably in habit. They may be scarcely foliose, or broad and leaf-like. They may have flat segments, or folded ones sometimes of boat-like appearance. The segments whether flat or folded may be reflexed and the whole pinnule rolled backwards like a tightly clenched fist, or they may be only slightly recurved or not reflexed at all. The species whose pinnules compare most closely with the fossils in general appearance appears to be the South American *A. gardneri* Hook., but in it the segments are fewer or more tightly enrolled, less rigid and less conspicuously jagged at the margins than in *A. poolensis* (Pl. 32, figs. 11–13). The species *A. schimperiana* Presl. from Angola also has closely folded pinnules in some herbarium material examined. A rare species from Madagascar *A. lanipes* Christensen is somewhat illuminating. Normally, its pinnules appear to be flattened in one plane and they are so described by Christensen. But a sheet No. 2798 (G. F. Scott Elliot Herbarium, Royal Gardens, Kew, 986) shows some pinnules definitely reflexed and rolled in varying degrees. In the most extreme instance the tightly rolled pinnules form sub-globular bodies 1·5 to 2 mm. in diameter. Perhaps this pinnule had become desiccated in life and had curled as the result, thereby protecting the sporangia on its lower surface. A similar tendency to protect by curling can be observed in British ferns growing in situations liable to periodic desiccation such as walls or crevices.

In *A. poolensis* the rolling of the pinnules appears to be a more or less constant character and it seems to be among terminal pinnules that rather flatter or less recurved specimens are found. Presumably the rolled up " bodies " were torn from the stipes by the battering they suffered from flood waters as they were swept to the places of deposition among angular quartz sand and coarse woody fragments.

A. lanipes is a peculiarly hairy species. *A. schimperiana* is also covered by a close felt of rather long hairs. The hairs of *A. schimperiana* are sparsely septate, long, swollen at the septa with a transverse diameter of 20 to 30μ across the cavity. Those of *A. lanipes* and *A. perrieriana* Chr. are similar so that they differ definitely from the fossil. Some Recent species have no hairs but are thickly beset with paraphyses like those of the fossil, e.g. *A. phyllitides* and *A. gardneri.* Some species, like the fossil, have both long hairs and turgid paraphyses, e.g. *A. schimperiana.* So far no non-septate hairs have been found in the few living species examined. Often the paraphyses in the living are less convex on one side than the other, or they may be concave on one side giving a curved form in profile. Others are symmetric. The basal end is not infrequently more rounded and blunter than the distal, and attachment is commonly by a short stalk either centrally placed or on one side. Paraphyses in *A. gardneri* were 110 × 55μ and in *A. phyllitides* 43 to 59μ long, 18·75 to 21·875μ broad. A paraphysis wall was measured in *A. schimperiana*. In optical section it was about 1–2μ thick.

The spores of the fossil, *A. poolensis*, appear to be unique in having a smooth glistening surface, but among the 115 living species of *Anemia* there are some whose spores are still unknown, and others which it has not been possible to examine. Nevertheless, many species were studied by Mr. Croft in the Herbarium of the Botanical Department of the British Museum (Natural History). The majority show highly characteristic ridged spores. The ridges may be smooth, tuberculate, or spiny. In some species the spore outline is more or less triangular, in others globose-tetrahedral. The size shows some little variation, e.g. 56 to 87·5μ in *A. gardneri* Hook. with a wall of about 4μ thick ; 75 to 100μ in *A. schimperiana* Presl. ; 93·75 to 106·25μ in *A. adiantifolium* Swz. ; 53 to 70·7μ in *A. perrieriana* Chr., wall 3 to 5·8μ thick ; about 81μ in *A. lanipes* Chr. Thus they tend on the whole to be larger than those of *A. poolensis* (50–60μ) which corresponds in size more closely with those of the American species *A. fremonti* forma *fertilis* Andrews. These according to Andrews & Pearsall (1941 : 169) show a considerable range from 25 to 47μ with an average of about 40μ ; some measured by the writer were as much as 50 or 53μ. The only smooth spores seen were immature examples of *A. perrieriana*. They had thick firm walls. One plant gave smooth spores only, but the next on the same sheet and no doubt from the same gathering had mature smooth-ridged spores. In this species, as Mr. Croft noted, the spores become thick-walled prior to the formation of ornament. The ridges vary in their distance apart in different species and also in their smoothness or degree of ornamentation as will be further discussed on p. 306.

Thus while the apical annulus indicates the family Schizaeaceae beyond doubt, the generic relationship calls for careful consideration. The reflexed enrolled fertile pinnules, annulus with a single row of cells, many-celled apical plate, and spore size, all point to *Anemia* as the nearest living genus, but the smooth unridged spores, differing from the mature spores of known species, are peculiar to the fossil and require some explanation. Can they possibly be regarded as immature spores like those of *A. perrieriana* described above ? or as mature spores, originally ridged but denuded in fossilization of an ornamental exine ? or should the fossils be separated on the grounds of smooth spores and non-septate hairs as a distinct genus ? While there can at present be no absolute proof of the generic status, the following considerations appear to the writer to justify the use of the name *Anemia* at least provisionally.

(1) The sporangia have constantly (although not invariably) dehisced naturally as if they were fully mature, but in undehisced specimens which have been protected by the sporangium wall the spores show the same smoothness.

(2) Smoothness of spore is an invariable feature in every pinnule examined and is seen not only in the Lake material but wherever the species has been found. It is

most improbable that only immature material would have been found in different localities and among so many different gatherings.

(3) Against the view that an ornamental exine has been lost in fossilization is the fact that a second species from Colwell (see p. 305) has typical ridged spores although this material has been far more macerated in fossilization than that now under consideration.

(4) In two fossil species of *Lygodium* hereafter described (pp. 308, 312), one has consistently smooth spores, the other has highly ornamental spores while the majority of living species of *Lygodium* have spores ornamented in various distinctive ways, though *L. elmeri*, for example, has smooth spores. It seems unreasonable, when smooth and ornamental spores can both occur within a related genus, to make smoothness a reason for separating *A. poolensis* generically from living *Anemia*. Possibly smoothness of spore is a primitive character which still persists in *Lygodium* to a small degree but is now lost in living *Anemia* so far as present knowledge goes. On the whole the balance of probability appears to the writer to justify reference of the fossil to the genus *Anemia* itself, although it must be admitted that the last word may yet remain to be said.

Anemia is an herbaceous genus. Some examples of habitat are here quoted from herbarium sheets at Kew: 1,500 metres in Angola, 3,000–4,000 ft. in Cuba, 1,500 ft. in Mexico, 3,900 ft. in New Granada, 5,000 ft. in Madras in the Nilghiri Hills. There are records of " shady rock crevices", "summit of dry mountain ranges", " wet rocks", " by the river ", " on rich moist shady banks under shrubs ", " moist calcareous river bluffs ", crevices in vertical side of limestone rock " and " rocky pinewoods ".

Anemia colwellensis n. sp.

(Pl. 35, figs. 39, 40, 42–53 ; Pl. 36, figs. 59–64 ; Text-fig. 2, 1)

Diagnosis. Fertile pinnule flat, about 2·5 mm. long, 1·7 mm. broad, with several (at least 8 ?) rounded alternating segments on opposite sides of a nerve. Free outer margins of segments sharply recurved on to the lower surface so as to give a smooth outline and to form a false fringed indusium. Main vein of pinnule sinuous. Nervation of segments flabellate, the nervules repeatedly forked and free. Upper surface smooth, without hairs ? Sporangia in two rows on the lower surface of each segment, sub-ovoid, somewhat laterally compressed giving a slight bisymmetry ; sessile, broadly attached by the whole breadth of the base. Length of sporangium very variable, maximum about 228 to 342μ ; breadth about 171μ. Annulus slightly bisymmetric, apical, conspicuous, formed by a single row of about 15 cells with extremely thick walls, occupying about one-half to one-third of the length of the sporangium. Trilete tetrahedral-globose spores ornamented with ridges which give the effect of tubercles where seen in profile at the margins. Diameter of spores 37·5 to 66·6μ, commonly 43 to 50μ. Height of spores from back to front 37·5 and 43·75μ in two specimens measured. Distance between ridges about 3 to 6·25μ. Paraphyses many among the sporangia, sessile or shortly stalked, about 114 to 120μ long, 48 to 72μ broad.

Holotype. V.31519–23.

DESCRIPTION. *Fertile pinnule* 2·5 mm. long, 1·7 mm. broad, having several (at least eight) short, rounded, closely contiguous segments situated alternately on the opposite sides of a nerve and inclined to it at angles of about 45° (Text-fig. 2, 1). The free outer margins of the segments are sharply recurved on to the lower surface thereby giving the peculiarly smooth, rounded outline shown and producing a flat false indusium on the lower surface, which partially covers the sporangia. The "indusium" is striate and marginally fringed, the alignment of the fringe being parallel with the planes of separation between the segments and corresponding with the cell-structure (Text-fig. 2, 1). Main vein of pinnule sunk in a sinuous channel on the upper surface, not actually seen on the lower where it was obscured by sporangia and masses of released spores. Nervation of segments flabellate, the venules being repeatedly forked and free as in the living *Anemia* and as in *Anemia* sp. 3 (see Pl. 36, fig. 65). Upper surface smooth and free from hairs, lower surface with turgid brown sub-fusiform paraphyses among the sporangia showing, when highly magnified, a curious transverse streaking perhaps due to stretching caused by crushing as it is not always apparent. The paraphyses may be shortly stalked but are usually rather broadly based. They are thin-walled and about 114 to 120μ long, 48 to 72μ broad (Pl. 35, figs. 47, 48). One fragment of pinnule segment showing the distal margin appeared to be at least two cells thick and displayed oblong, almost rectangular, cells about 6 to 12μ in diameter with very fine closely digitate (sinuous) walls. The free ends of the nervules in this fragment were about 12μ apart.

The sporangia (Pl. 35, figs. 39, 40, 42–46) are large although they vary considerably in size with the degree of development and possibly with their position on the pinnule. The largest are about 228 to 342μ long and about 171μ broad. They are sub-ovoid but somewhat flattened so as to be bisymmetric, sessile and broadly attached by the whole breadth of the base, tearing away from the surface of the pinnule in a ragged manner often with fragments of epidermis still adhering. The apical annulus is in some cases somewhat bisymmetric owing to the flattening, it is a conspicuous feature sometimes bulging out beyond the sporangial wall below, occupying from one-third to one-half the length of the sporangium. It consists of a single row of at least 15 long narrow cells with straight thick walls which fork conspicuously at their lower extremities where they alternate with the thinner cells of the sporangial wall. Dehiscence longitudinal with stomium long and conspicuous. Its cell-structure is obscure owing to the deneseness of the material and its broken character. It appears to have been directed towards the margin of the segment when in the position of growth. Apical plate multicellular, delicate, of angular equiaxial cells. Cells of sporangial wall elongate parallel to the major axis of the sporangium (Pl. 35, fig. 45), about 24μ broad, straight superficially, unevenly thickened so as to have a "beaded" appearance when seen from the interior. They contain numerous rounded or angular bodies which may have been chloroplasts but they are now heavily pyritized and glistening (Pl. 35, figs. 42, 43, 45). Spores (Pl. 35, figs, 49, 53; Pl. 36, figs. 59–64) trilete, tetrahedral-globose, somewhat triangular in outline, conspicuously but finely ridged, the ridges when seen in profile giving a false tubercled appearance to the outline of the spores. Distance between the ridges varies in different parts of the spore and may be from 3 to 6·25μ. The distal ends of the rays sometimes fork, and splitting may occur along the rays (Pl. 36, fig. 62). The diameter of the spores varies from 37·5 to 66·6μ and is commonly from 43 to 50μ. The height from the dorsal to the ventral side is more or less equal to the diameter. Two measurements of height were 37·5 and 43·75μ.

REMARKS. One fertile pinnule more or less complete. This minute fragment was so tender that it fell to pieces on attempting to lift it on to a slide. Fortunately a drawing of the under surface had been made and a preliminary examination of both surfaces. Even more fortunately it was possible to make several slides of the remains showing sporangia, annuli and spores. Paraphyses are also preserved on the slides, but there are no indications of a felt of hairs. A small fragment of the pinnule itself is mounted on one slide showing nerves and cell-structure. The slides are rather opaque as the material was too scarce to risk destroying it by more than a slight degree of maceration in nitric acid. The character of pinnule, sporangia and and spores indicates the genus *Anemia* without question. Fortunately, in this case, the spore ornamentation is typical of *Anemia*. It is significant that the ornamentation is preserved in spite of the rotten and fragile state of the pinnule fragment, so much more rotted in fossilization than the pinnules of *A. poolensis*. The flat unreflexed pinnule with fringed false indusium formed by the reflexed margins of the short smooth-edged segments, the short broadly attached sporangia without hint of narrowing or arising from a stalk, the large deep annulus and the ridged spores, distinguish this species without any doubt at all from *A. poolensis*. Study of some of the many living species of *Anemia* indicates that the ridges on the spores vary to some extent in different species in their distance from one another and in their ornamentation. Thus in *A. schimperiana* the ridges are simple, not tubercled, and the spores sharply triangular with clear translucent rounded projections at the angles. The ridges are about 6μ apart. In *A. gardneri* the ridges bear contiguous tubercles which are a conspicuous feature, the tubercles being about 6μ in diameter. In *A. adiantifolium* the spore has round translucent angular projections, the ridges are smooth, and about 10μ apart. In *A. lanipes* they are sharp and thin, and may be 6μ apart, although sometimes closer. *A. aurita* Sw. has ridges with tubercles, *A. anthriscifolia* Schrad. has smooth or minutely echinulate ridges. In *A. perrieriana* the surface of the spore is ridged coarsely. *A. affinis* Bak. has large spiny spores. The ridges on the fossil *A. fremonti* forma *fertilis* are about 2·1 to 2·5μ apart. *A. phyllitides* has spines or long pointed tubercles arranged on ridges in the mature spores. It would involve prolonged study to attempt any sort of classification of the genus by its spore characters or even to prove conclusively that such was possible. Such a study cannot be undertaken for the purposes of this paper but knowledge of *Anemia* is incomplete without it.

The pinnule segments of the fossil recall *A. imbricata* Sturm. (Brazil), *A. ferruginea* —a hairy species from Central America (= *A. fulva* Hook.), the flat pinnules of *A. lanipes* (Madagascar), and *A. tomentosa* Sw. (warm America from Mexico and the Antilles to Peru and the Argentine). More fossil material is needed to complete the record of this interesting fern. But whatever view may be taken of the generic position of *A. poolensis*. the presence of *Anemia* in Southern England is indisputably established by the tiny fertile fragment described above as *A. colwellensis*.

Anemia sp. 3

(Pl. 36, fig. 65)

1926. *Filix incertae sedis*, sp. 5 ; Reid & Chandler, p. 39, pl. 1, figs. 10, 11.

To the description previously published may be added the additional fact that some of the pinnules are asymmetric. There can be little doubt that this fern belongs to *Anemia*. For details of pinnules and nervation see Reid & Chandler (1926). The characters of these barren pinnules closely resemble those of the pinnule segments of *A. colwellensis* both in the smoothness of their margins and in the flabellate nervation. It is interesting to speculate whether the Bembridge specimens can possibly be barren material of *A. colwellensis*, but there the matter must rest until further evidence is available to prove or disprove their specific identity.

Genus *LYGODIUM* Swartz

Lygodium prestwichii (Gardner & Ettingshausen)

(Pl. 36, figs. 66–69)

1854. *Asplenium* sp.? Prestwich, p. 156, pl. 3, fig. 6.
1880. *Pteris* (?) *prestwichii* Gardner & Ettingshausen, p. 53, pl. 10, fig. 8.
1886. *Lygodium prestwichii* (Gard. & Ett.) Gardner, pp. 400, 401, 403, pl. 2, figs. 2–4.

Diagnosis. Pinnae simple, elongate lanceolate-linear or cleft. Veins diverging at a sharp angle from the midrib, crowded, forking once or twice, midrib considerably thinned towards the apex. Fertile pinnules borne around the toothed margins of the barren pinnules ? Sporangia, spores and fertile pinnules unknown.

Neotype. V.24862.

Remarks. Fragments of this fern were found at Counter Hill, Lewisham, by Prestwich (1854, pl. 3, fig. 6 ; see also Gardner & Ettingshausen 1880, pl. 10, fig. 8), and by Gardner at Croydon and Woolwich (Gardner 1886, pl. 2, figs. 2–4). Gardner considered all these specimens as identical specifically after comparing his own material with that of Prestwich (1886 : 403). He regarded the species with its sparsely-toothed pinnules as characteristic of the Woolwich Beds and as quite distinct from *Lygodium kaulfussi* from Bournemouth. One fragment figured by Gardner (1886, pl. 2, fig. 2) shows a " toothed " margin, the projections being (so he states) the bases of fertile segments removed in fossilization. Unfortunately the Prestwich pinnule from Lewisham seems to have disappeared (Gardner & Ettingshausen, 1880 : 53) and even Gardner's Woolwich and Croydon specimens cannot now be traced. It is therefore fortunate that a few fragmentary pinnules with toothed margins which apparently belong to the same species were collected more recently by the late H. C. Berdinner in beds at Newington. From the locality and their appearance they may be presumed to be of Woolwich age. They are impressions only representing fragmentary pinnules. One (V.24862) with counterpart, shows two lobes of a pinna, one lobe being much puckered and folded longitudinally. The midrib is stout and tapering, rounded and prominent on the lower surface (represented by a furrow on the impression). The nerves are about 0·6 to 0·75 mm. apart where they spring from the midrib. They are represented on the impressions by thin raised thread-like lines. The marginal teeth are well preserved in parts (Pl. 36, figs. 66–68) ; the margins of the frond were thickened, especially at the tips of the teeth. There is nothing in this specimen, or in V.24861 which also shows teeth, to indicate that the teeth were associated with fallen fertile pinnules as Gardner supposed, and on the whole the appearance of the two specimens is against this interpretation. Nevertheless it is possible that these particular fragments happened to have been barren, whereas if they had been fertile the association of teeth and fertile pinnules might have been shown. But whether the teeth were, or were not, associated with fertile pinnules, it seems clear at least that their presence indicates that in the Woolwich Beds there was a species quite distinct from the Bagshot *L. kaulfussi* with its entire-margined barren pinnules and its much-branched fertile pinnules which apparently were borne in a panicle at the tips of barren fronds and not around their margins. In describing the species Gardner (1886 : 403) recorded that " the pinna was simple or cleft into two or more lobes". The veins were free, diverging at a sharp angle from the midrib, forking once or twice. Prestwich figures nerves about 0·75 mm. apart near their origin on the midrib.

Gardner thought the species indistinguishable from *Lygodium japonicum* Sw. a native of Japan, China, Ceylon, Java and the Philippines, but this is a curious conclusion for it does not accord with his views about the position of the fertile pinnules of the fossil. In living *L. japonicum* they are borne in clusters at the tips of the barren pinnules as they are also in *L. articulatum* Rich. and *L. palmatum* Sw. *L. prestwichii* rather resembles the other group of living species in which the strap-shaped pinnules whether simple or parts of subdivided pinnae carry the fertile pinnules around their margins, an arrangement seen, for example, in the living *L. flexuosum* (L.), *L. volubile* Sw., *L. circinnatum* (Burm.) and *L. salicifolium* Presl.

Lygodium is a climbing fern of tropical and subtropical lands in both hemispheres. In North America it occurs in Florida and Massachusetts in woodlands and in lowland areas of New Jersey. In South America it extends to southern Brazil east of the Andes but less far south on the west of the mountain range. Professor Halle (1940) points out that his fossil species *L. skottsbergii* is found 30° south of the present extension of the genus. In the old world the genus goes north into China, e.g. 500 metres above sea level in Szechuan and southward to New Zealand, occurring throughout the whole of the tropical belt. Some species have pinnules with toothed margins and in others the margin is entire.

Lygodium kaulfussi Heer

(Pl. 37, figs. 70–83 ; Pl. 38, figs. 84–87)

1861. ? *Lygodium kaulfussi* Heer, p. 409, pl. 8, fig. 21 ; pl. 9, fig. 1.
? 1879. *Asplenites prae-allosuroides* Gardner & Ettingshausen, p. 34, pl. 3, figs. 1, 2.
1880. *Lygodium kaulfussi* Heer : Gardner & Ettingshausen, p. 47, pl. 7, figs. 1, 3–8 ; pl. 10, fig. 11.
1882. *Lygodium kaulfussi* Heer : Gardner, pp. 67, 68.
1886. *Lygodium* sp., Gardner, pp. 401, 404, pl. 3, fig. 9.

DIAGNOSIS. Barren fronds simple or deeply palmately divided, tapering to the base. Fertile pinnules borne in a sympodially branched tuft with segments in pairs or threes. Spores trilete and tetrahedral-globose, shining, smooth or minutely granular, about 75 to 112μ in diameter.

NEOTYPE. V.14962.

DESCRIPTION. Barren pinnules have been described and figured from Bournemouth and Studland, and two small tufts of fertile pinnules from Bournemouth (Gardner & Ettingshausen, 1879, 1880; Gardner, 1886). Gardner states that the barren pinnules from Studland were very near to those from Bournemouth but with "much closer veins", and suggested that the Studland specimens were intermediate in form between *L. kaulfussi* from Bournemouth and *L. prestwichii* from the Woolwich Beds. It is not clear from his statement whether he really regarded the Studland material as belonging to a species distinct from *L. kaulfussi*. But fertile pinnae with spores now afford evidence that the Studland and Bournemouth material is specifically identical (cf. Pl. 37, fig. 78; Pl. 38, fig. 86 from Branksome Dene, with Pl. 37, figs. 72, 74, 80–83; Pl. 38, fig. 85 from Studland). Moreover, the recently collected barren pinnules from Studland agree closely with some of Gardner's Bournemouth specimens. The differences of nervation which he noted are therefore probably individual variations with no specific significance. This view is supported by the variations which can be found in living *Lygodium* species.

Gardner & Ettingshausen's description of the Bournemouth fronds is full and detailed, and it is not necessary to repeat it, but Gardner gave only the briefest account of the single Studland fragment figured. The following additional details based on the fresh material may therefore not be out of place.

The barren fronds are not infrequently to be found as perishable impressions in the lower part of the soft laminated dark grey clays about 4 to 5 ft. above the sandrock, i.e. within the lowest 100 ft. of the Lower Bagshot Beds. Often the impressions are covered by decayed remains of actual fronds which quickly crack and crumble on exposure to air. The few pinnules so far seen are variable in shape and sometimes divided near the base (Pl. 37, fig. 70). The lobes may be short or long and lanceolate, obtuse at the apex, tapering somewhat towards the base, with entire margins. The primary nerves are stout but become attenuated above, the secondary nerves are close together, about 0·4 to 0·5 mm. apart, given off at acute angles, thrice forked, sharply defined.

Fertile pinnules (Pl. 37, figs. 72–78). The specimen figured from Bournemouth (Gardner & Ettingshausen, 1880, pl. 10, fig. 11) shows a repeatedly divided pinna with stalked pinnules which are linear-elongate and serrate along the margins. Gardner & Ettingshausen (1880 : 48) state that the pinnules in the upper part were "solitary or undivided, but in the lower part two or three occur together or are twice or thrice divided". This two- or three-fold division may also be seen in the living *L. articulatum* Rich. The midribs are sinuous and the rachides unwinged. Gardner did not record sporangia nor spores, but a preparation from V.14962 (the neotype) has revealed the presence of spores identical with those described below.

In 1882 (p. 68) Gardner reconsidered the specimen which he and Ettingshausen (1879) had named *Asplenites prae-allosuroides* (V.14968), and decided that it was a fertile frond of *Lygodium* with " exceptionally abbreviated pinnules". No spores could be obtained from this specimen when it was re-examined recently, and in view of the difference in form of the fertile segments its identity with *L. kaulfussi* must remain doubtful.

The fertile pinnules from Studland are well preserved. They were isolated from the matrix by boiling, washing and sifting, and were then examined microscopically. Only detached solitary fertile pinnules have as yet been seen. When perfect they are petiolate and, as in the Bournemouth specimens, without any wing-like extension of the lamina along the stalk. They are linear-elongate, obtuse at the apex, serrate along the margins, while the markedly sinuous midrib is sometimes very conspicuous, although only slightly raised, on the upper surface; it is often prominent on the lower surface which may have a longitudinal facet on each side of it (Pl. 37, figs. 73, 75). The epidermis is formed of deeply interlocking cells with beaded appearance due to unevenly thickened walls (Pl. 37, fig. 79). The diameter of the largest cell seen including the digitations was 0·048 mm. The sporangia are oval, flattened, sunk in oval hollows on the underside of the pinnules, concealed by overlapping bracts or indusia. They remain obscure even in macerated specimens because of the thick and opaque character of the bracts and pinnules which surround and protect them. They diverge in a pinnate manner from the midrib, one sporangium corresponding to each tooth of the serrate margin. The walls of the sporangia are usually ruptured so that as a rule the form, structure and annulus are destroyed or masked, especially if covered and surrounded by a mass of liberated spores. After maceration, remains of the annulus can sometimes be seen with thick-walled more or less parallel-sided elongate cells.

The spores (Pl. 37, figs. 80–83 ; Pl. 38, figs. 84–87) are numerous, globular-tetrahedral with clear fine triradiate marks, the rays sometimes forking slightly at their free extremities. The surface is shining and smooth or very finely granular resembling figures of *L. skottsbergii* Halle (1940, pl. 1, figs. 9, 10) from supposed Eocene beds of Coronal, province of Concepcion, South Chile, South America. A few tubercles or granules are sufficiently prominent to be visible in profile, but they are probably fragments accidentally adhering to the surface, for although apparent when the spores are first mounted in glycerine, they quickly disappear leaving a perfectly smooth surface. The diameter of the spores varies from 75 to 112μ, and is frequently about 100μ when uncollapsed, very rarely larger. The thickness of the coat in the largest spore seen was as much as 6μ. More frequently it is only about 3μ in optical section. The length of the fertile pinnules is about 4·5 mm. ; breadth about 1·5 mm. Length of toothed segments of fertile pinnules about 0·5 mm. Identical fertile pinnules with identical spores were also found at Branksome Dene, Bournemouth Freshwater Beds (Pl. 37, fig. 78 ; Pl. 38, fig. 86).

It must be stressed that barren and fertile material have not yet been found in organic connexion but as their association in the same beds at Studland almost certainly points to derivation from a single species, they are so regarded and described here. The fertile pinnules and spores afford conclusive evidence that the Studland and Bournemouth material is specifically identical, while the barren fronds from the two localities appear to the writer to agree also.

An isolated spore, apparently of this species, has also been found in the Cliff End Beds of Mudeford (Auversian ?) (Pl. 38, fig. 87). Halle (1940: 261) pointed out that the type of *L. kaulfussi* Heer was an indeterminable and useless fragment whereas the numerous fossil records of *L. kaulfussi* are, in fact, based on the well-preserved English Eocene fronds unfortunately identified with the useless Skopau type. Hence, he suggested, Gardner's specimens may, for practical purposes, serve as the type of the species *L. kaulfussi* and the specimen British Museum (Natural History) No. V.14962 is here designated as the Neotype.

The Studland and Bournemouth fossils have been united as a single species only after careful consideration of the evidence afforded by the fertile pinnules from both localities following upon a study of the spores of twenty-six living species. This investigation was made possible by the kindness of Mr. A. H. G. Alston of the Botanical Department, British Museum (Natural History). It strongly suggests that when their characters have been fully studied they will prove to be sufficiently distinctive for use in specific determination in the majority of species. But much time and labour would be required in order to work out the spore characters of the genus in a really satisfactory manner. For in every species it would be essential to examine a wide range of material from different plants and localities to find out the true limits of variation of the spores within each. Moreover the determination of the Herbarium material itself would have to be checked. As an illustration of the nature of the problem it is perhaps sufficient to quote the cases of *L. volubile* Sw. or *L. circinnatum* (Burm.) which displayed considerable variations of spore character on different sheets and which perhaps include more than one species in each case. On the other hand readily recognizable species such as *L. reticulatum* Schk., *L. articulatum*, *L. japonicum*, *L. scandens* (L.), *L. polymorphum* (Car.), *L. smithianum* Pr. and *L. palmatum* Sw., each have distinctive spores which appear constant in character. The spores of different species may vary in form, e.g. they may be more or less conical, or sub-globular, or more or less sharply angled. They also vary in size from about 40μ in diameter in *L. borneense* and *L. elmeri*; 40 to 50μ in *L. japonicum* and *L. polymorphum*; and 80 to over 100μ in *L. hians*, *L. articulatum*, *L. reticulatum*, *L. cubense*, *L. merrilli* and *L. lucens*.

Whereas by far the greater number of living species have spores which are ornamented in a greater or lesser degree they do vary considerably in surface ornamentation and thickness of spore wall, while a few species are smooth and shining. Thus *L. elmeri* is smooth and fairly thick-walled with only very occasional scattered minute tubercles. *L. polymorphum* is thin-walled and finely granular all over. *L. reticulatum* has a coarse reticulation of the surface, and *L. scandens* is somewhat similar with a series of deep pits. In *L. articulatum* the whole surface is covered by low, rounded, contiguous tubercles which diminish in size between the arms of the three-rayed scar on the ventral surface. *L. japonicum* is evenly covered with regular, low, rounded, contiguous tubercles smaller than those of *L. articulatum*. *L. borneense* is thin-walled with small distinct close-set tubercles. *L. merrilli* has larger but quite distinctly separated tubercles. In *L. smithianum* and in one sheet attributed to *L. volubile* (Nardil, 1891) from Trinidad, the spore has a fairly broad equatorial flange, irregular scattered large wart-like tubercles sometimes as much as 10μ broad, with finer tubercles between, especially on the surface in the angles of the rays.

The spores of *L. kaulfussi* from Studland and Bournemouth are characterized by their large size, often 100μ or larger, thin walls, and smooth or very finely granular surface. These characters combined, together with the globose-tetrahedral shape, appear to distinguish them from any living *Lygodium* seen. As already mentioned (p. 310) smooth-walled spores of exactly similar appearance and comparable size (65–105μ commonly 85μ) occur in Halle's species *L. skottsbergii*. The fertile fronds of this species appear to have had a mode of growth in a tuft like that of *L. kaulfussi* but show a much reduced lamina on the sides of the rachides, absent (possibly through lack of preservation) in *L. kaulfussi*. Halle separated his species from *L. kaulfussi* on account of the shorter, broader segments of the barren pinnules, their asymmetrical shape and truncate base, and especially on account of the number of segments (three). But he writes that the fertile specimens of *L. skottsbergii* might belong to *L. kaulfussi*. There is certainly a close general resemblance between the two, and this is supported by the character of the unusually smooth spores which are also comparable in size and shape. They are certainly more similar to one another than to any living species, and it is tempting to think that they *may* be identical and that such variations as occur may even be the result of different climatic or ecological conditions.

A few smooth spores and barren and fertile pinnules attributed to *L. gaudini* Heer are figured by Gilkinet (1922 : 5, pl. 14, figs. 2–9). Unfortunately the figures show little detail and spore dimensions are not given. The material is from beds of uncertain age in the argiles of Andenne (Aquitanian or Lower Miocene ?) yielding also a number of Bovey Tracey species. There is no obvious difference from *L. kaulfussi* although Gardner regarded Heer's two species (*L. kaulfussi* and *L. gaudini*) as quite distinct. Possibly in view of Halle's comment on the first named (see p. 311) they should not be separated. It is tempting to wonder whether in view of the preceding remarks *L. kaulfussi* may have been a plant of very wide range, particularly in Eocene times, possibly even a persistent relic of the ancient more or less world-wide genera of the tropical and subtropical province.

While, however, the specific relationship of these forms from wide-spread localities must await further confirmation from an exhaustive comparative study of the actual fossil material, there can be no reasonable objection to uniting the Studland and Bournemouth fossils of which such a study has been made.

The general distribution of *Lygodium* is given on p. 308.

Lygodium poolensis n. sp.

(Pl. 38, figs. 88–96)

Diagnosis (based on spores). Spores trilete, subglobular-tetrahedral, ranging from about 50 to 70μ in diameter, commonly about 65 to 68μ. Depth from the ventral to the dorsal side about 41–42μ. Surface ornamented with numerous flat-topped tubercles about 4μ in diameter below, projecting conspicuously from the surface for about 4μ as seen in optical section.

HOLOTYPE. V.31533.

DESCRIPTION. *Barren pinnules* unknown.

Fertile pinnules known only from a single naturally macerated fragment about 1·75 mm. long and from a detached spore on a slide of *Anemia.* Maceration has removed the lamina leaving the slightly sinuous midrib and a few attached solitary sporangia which are borne on it in a pinnate manner at the ends of the nervules. One sporangium (Pl. 38, figs. 88, 89) is perfect, four others are incomplete, two of them being almost entirely broken away. The perfect sporangium is broadly bolster-shaped or sub-ellipsoid with a large spreading annulus on one side near the proximal end. It was very clearly displayed when the specimen was first placed in nitric acid and can still be distinguished when examined by strong reflected light against a white background. The sporangium is about 0·55 mm. long, 0·3 mm. broad. The annulus about 0·34 mm. in maximum diameter extending for over half the length of the sporangium. It is only about 0·17 mm. in depth.

Spores numerous, trilete, tetrahedral-subglobose, low conical or low triangular-pyramidal having a sub-circular or rounded triangular outline. Triradiate mark clear, sharp and fine, the rays about 18–25μ in length. Surface highly ornamental having a series of deep pits whose coalescent walls produce the effect of rather flat-topped tubercles (Pl. 38, figs. 90–96). Diameter of tubercles often about 4μ ; height 2·5 or 3 to 4μ. About four tubercles occupy a square of about $12·5 \times 12·5\mu$. The tubercles project conspicuously at the circumference of the spores when seen in profile. Typical spore dimensions are 65μ ; $70 \times 50\mu$; $65 \times 60\mu$; $55 \times 68·7\mu$; $66 \times 50\mu$; $66 \times 57\mu$; $57 \times 54\mu$; $63 \times 48\mu$. One spore which measured $68·7\mu$ in diameter was $41·25\mu$ in height (dorsi-ventral profile) ; thickness of spore walls where measured about 4μ.

REMARKS : As already noted there are some grounds for regarding spores of *Lygodium* as of use in specific determination. Tubercled spores similar in character to those of the fossil occur in very few living species but are present in *L. scandens* Sw. and *L. reticulatum* Schk. These two species are grouped together by Diels on account of their reticulated spores which appear to separate them from other species. A sheet of *L. scandens* (Thwaites 1404) in the Herbarium of the Botanical Department, British Museum (Natural History) showed spores varying in diameter from about 66 to 84μ, and in another which more closely resembled the fossil (Ross 123 from Nigeria) spore diameter was 60 to 84μ and the height about 41μ (Pl. 38, figs. 97–101). The tubercles appeared somewhat less conspicuous and prominent at the margin of the spore as well as rather coarser and more rounded than in the fossil. A sheet of *L. reticulatum* (Compton 244) had larger spores, 80 to 110μ in diameter, while another sheet from New Hebrides (McGillivray 1860) showed similar variations of size. The tubercles were considerably less prominent at the margin than in the fossil.

Diels gives the geographical range of *L. scandens* as West Africa, Further India to Chitral, South China, Malaya to North Australia, and of *L. reticulatum* as North Australia, Melanesia and Polynesia. Hence the fossil *L. poolensis* appears to be related to an essentially tropical old world sub-division of *Lygodium*. In *L. scandens* the nerves of the barren pinnules are free ; in *L. reticulatum* they anastomose. A note on the sheet of *L. scandens*, from which spores are illustrated, states that it occurred in swamp forest near sea level in Nigeria. *L. poolensis* is readily distinguished by its spores from the smooth-spored *L. kaulfussi*.

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PLATE 32

Anemia poolensis n. sp.

FIG. 1. A recurved pinnule with attachment to stipe at (*a*). Several segments are seen directed downwards with the sporangia on the lower surface projecting along their margins. The transverse and longitudinal alignment of the cells over the middle of the segments on the upper surface is clearly seen. × 26. V.31495.

FIG. 2. A single boat-shaped segment of a pinnule, side view with upper surface on the right. It shows the crowded sporangia arranged in two rows on the under surface. × 15 (now disintegrated).

FIG. 3. The same, enlarged. The apical annuli with elongate cells can be distinguished. × *ca.* 35.

FIG. 4. A segment, lower surface with distal end at the top of the figure. It shows the sporangia springing from the pinnule close to the nervule. Annuli of sporangia and elongate cells of sporangial wall and pinnule are visible. × 50. V.31496.

FIG. 5. Segment attached at (*a*), dorsi-lateral view showing the apices of three sporangia which project beyond the margin of the segment. Two have gaped longitudinally. The sporangium at the distal end (top in figure) is shown in Pl. 33, fig. 15. ×28·5. V. 31497.

FIG. 6. A pinnule segment covered with a felt of pointed hairs. Attachment at (*a*). × 50. V.31498.

FIG. 7. A detached sporangium showing the contraction to the attachment and short stalk at (*a*). The dense region of the annulus is visible at the opposite extremity. × 150. V.31499.

FIG. 8. Another with dark thick-celled annulus and attachment (twisted) at (*a*). The thin cells of the sporangial wall show the bead-like thickening which is present on the inner surface × 150. V.31500.

All the above are from Lake, Dorset.

FIG. 9. Apical view of a disrupted annulus with stomium at (*s*). Remains of the torn sporangial wall close to the line of the stomium are seen at (*spg*). × 150. V.31516. Sandbanks, Dorset.

Fig. 10. Apex of a sporangium, side view, showing the thick-walled annulus and some of the contained spores. Granules in the cells of the sporangial wall chiefly below the annulus appear to be chloroplasts. × 150. V.31512. Branksome Dene, Dorset.

Anemia gardneri (Recent)

FIG. 11. Part of a pinna to show the habit, with tertiary reflexed pinnae arising from the stipe and bearing reflexed enrolled pinnules. × 5·5.

FIG. 12. The same, opposite side. × 5·5.

FIG. 13. The same (upper part) to show the recurved pinnules more clearly. × 15.

ANEMIA POOLENSIS A. GARDNERI (Recent)

PLATE 33

Anemia poolensis n. sp.

FIG. 14. Apex of a dehisced sporangium showing the stomium and the thick-walled annulus. A few cells of the broken apical plate still adhere to the upper ends of the annulus cells. A few cells of the sporangium wall with bead-like thickening are seen at *sw*. × 150. V.31501.

FIG. 15. Apex of a sporangium which has dehisced longitudinally. It shows clearly the ring of thick-walled cells which form the annulus and the thin-walled cells bordering the stomium (*st*). The multicellular apical plate lies between the upper ends of the annulus cells. Spores still remaining within the sporangium are visible at *s*, *s*, *s*. × 161. This sporangium is the topmost one shown in Pl. 32, fig. 5. V.31497.

Fig. 16. The apex (side view) of a sporangium (*sp* 1) of which the apical plate is obscurely seen at (*a*). (*an*) is the thickened annulus. Part of the annulus of another sporangium with its apex to the right is at (*sp*2). × 150. V.31502.

FIG. 17. The sporangium (*sp*1) in fig. 16 showing the cells of the burst apical plate (*a*) between the upper ends of the thickened annulus cells. × 400.

FIG. 18. Part of a pinnule segment. Two paraphyses (*p*, *p*) are still in position on the under surface which faces the camera. × 75. V.31503.

FIG. 19. A detached almost unmacerated paraphysis showing the inflated form and opaque character before maceration. × 400. V.31504.

FIG. 20. Another large detached paraphysis which has begun to collapse and crumple as the result of maceration. The opaque lining has begun to break down as can well be seen at the proximal end (*p*). The point of attachment was at (*a*). × 400. V.31499.

FIG. 21. Another (still opaque) showing the point of attachment below at (*a*). × 400. V.31505.

FIG. 22. Another after treatment, translucent but still inflated although somewhat crumpled. × 400. V.31506.

Anemia schimperiana (Recent)

FIG. 23. A Recent paraphysis for comparison (Gossweiler 9705). × 400.

Anemia poolensis n. sp.

FIG. 24. A spore showing the smooth inflated form and (obscurely) the three rays. × 400. V.31507.

FIG. 25. Another, partly out of focus, showing two of the three rays clearly. The smooth inflated form is again shown. × 400. V.31505.

FIG. 26. The same spore with different focus. The thickness of the wall and smooth rounded form are indicated. The rays are out of focus. × 400.

FIG. 27. Another spore showing the triradiate mark. The forking of the free ends of the rays is clearly visible. × 400. V.31508.

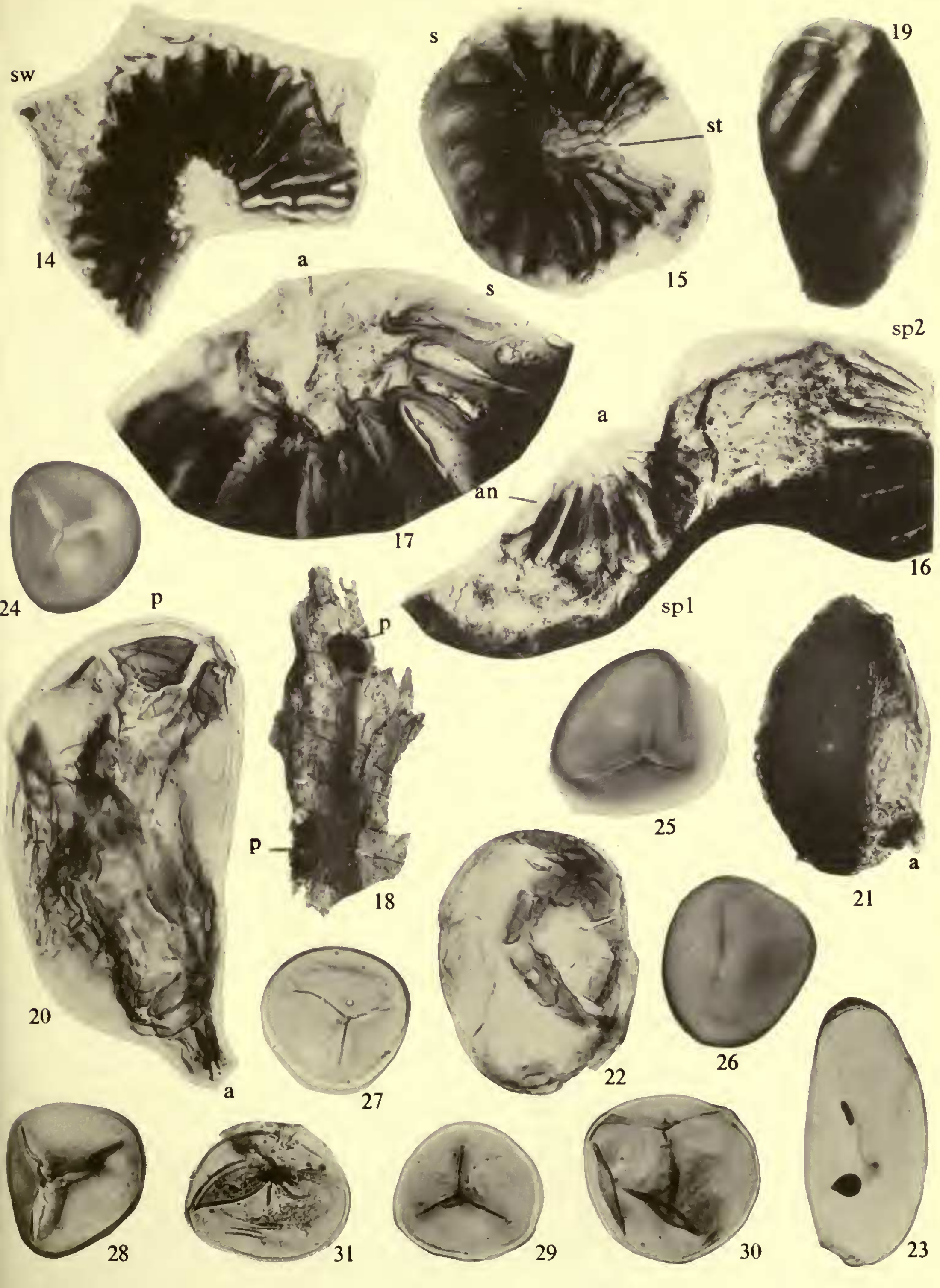
All the above, except fig. 23, are from Lake, Dorset.

FIG. 28. A spore slightly collapsed showing the three rays along one of which the spore has burst. × 400. V.31517. Sandbanks, Dorset.

FIG. 29. A spore showing the three rays very clearly. × 400. V.31513. Branksome Dene, Dorset.

FIG. 30. A somewhat crumpled spore. × 400. V. 31513. Branksome Dene, Dorset.

FIG. 31. A somewhat crumpled detached spore almost certainly of this species. × 400. V.31518. Alum Bay, Isle of Wight.



ANEMIA POOLENSIS, A. SCHIMPERIANA (Recent)

PLATE 34

Anemia poolensis n. sp.

FIG. 32. Microtome section through a pinnule segment showing more than one layer of thin-walled cells. × 150. Section now disorganized. V.31509.

FIG. 33. Microtome section across a recurved fertile pinnule. It shows the overlapping of pinnule segments, sporangia packed with spores close together on the lower surfaces of the segments, and the thick-walled cells of annuli usually in section. × 50. V.31510.

FIG. 34. Part of another section across the same pinnule. Two overlapping segments are shown, many cells thick in this part of the pinnule. One sporangium in section and parts of two others, one with annulus displayed. × 150.

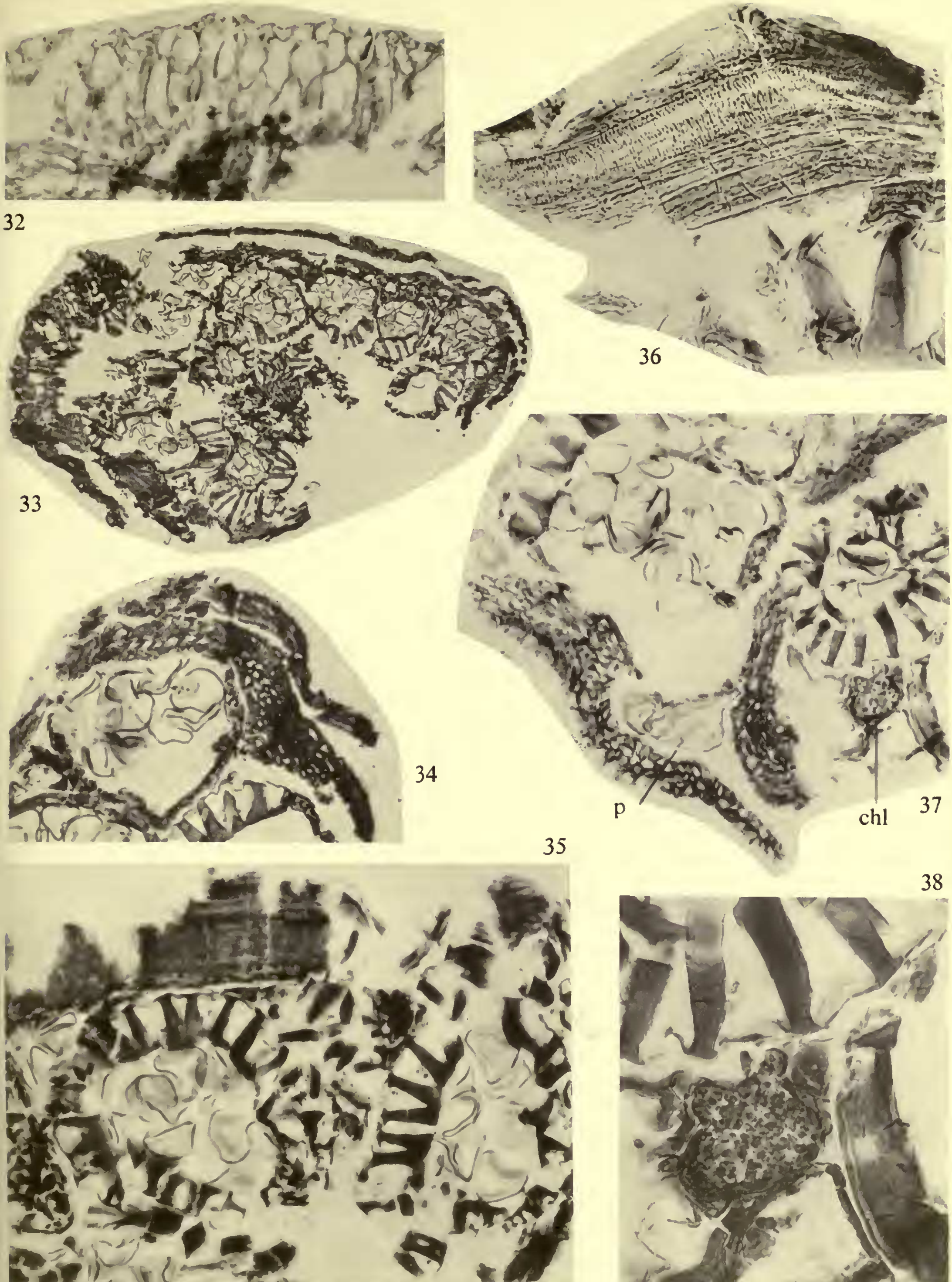
FIG. 35. Another microtome section showing the annuli and spores of two sporangia. × 150. Section now disorganized. V.31509.

FIG. 36. Microtome section showing thickened tracheids in the pinnule segment. Part of an annulus is seen below. × 400. V.31506.

FIG. 37. Another section of the same pinnule showing overlapping pinnule segments, many cells thick proximally, thinning to a few cells thick only, distally. A partly collapsed paraphysis (*p*) is seen arising from one of the segments. Two sporangia are visible in section, that on the right showing much of the annulus. Below it is a small patch of chloroplast granules (*chl*) probably inside one of the cells of the sporangium wall. Spores are visible in the sporangia. × 150. V.31506.

FIG. 38. Part of the same, enlarged, to show the group of chloroplasts just below the thick-walled cells of the annulus. × 400.

All the above are from Lake, Dorset.



ANEMIA POOLENSIS

PLATE 35

Anemia colwellensis n. sp.

FIG. 39. Annulus, imperfect, from above. × 150. V.31519.

FIG. 40. Part of another annulus, torn and distorted, from above. × 150. V. 31520.

Anemia poolensis n. sp.

FIG. 41. Annulus, from above, for comparison. The cells which have the appearance of an apical plate are probably a displaced fragment of sporangial wall. Each shows one dark spot (chloroplast?). × 94. V.31514. Branksome Dene, Dorset.

Anemia colwellensis n. sp.

FIG. 42. Upper half of a sporangium with apical annulus, side view. Two or three cells of the apical plate remain. The cells of the sporangium wall immediately below the annulus show numerous opaque grains of pyrites, perhaps pyrites replacements of chloroplasts. × 94. V.31521.

FIG. 43. An enlargement of the same. (*ap*) cells of apical plate. × 150.

FIG. 44. A somewhat distorted sporangium, side, showing the apical annulus above, and the torn sporangium wall below. × 150. V.31520.

FIG. 45. Remains of two sporangia (*sp* 1, *sp* 2) seen from the side. In both the annulus is dense and black, their cells being almost indistinguishable. The thinner sporangium wall is preserved below the annulus in one specimen (*sp* 2) only. A few pyrites grains (chloroplasts?) are seen. Spores are visible at (*s*, *s*). × 150. V.31522.

FIG. 46. An annulus, from above. The ring of cells is ruptured and the apical plate destroyed. A spore is seen in the gap. × 150. V.31520.

FIG. 47. A paraphysis (*p*) still attached to a fragment of leaf. × 400. V.31520.

FIG. 48. Another isolated paraphysis. × 400. V.31520.

FIG. 49. A spore showing the ridges. × 200. V.31522.

FIG. 50. The same (partly reflected light) showing the straight untubercled character of the ridges. × 400.

FIG. 51. The same (transmitted light) focused to show the triradiate mark. × 400.

FIG. 52. The same focused to show spore outline and thickness of wall. × 400.

FIG. 53. Another spore, side view. × 400. V.31522.

All the above, except Fig. 41, are from Colwell Bay, Isle of Wight.

All specimens of *Anemia colwellensis* are from the holotype.

ANEMIA COLWELLENSIS, A. POOLENSIS

PLATE 36

Anemia poolensis n. sp.

FIG. 54. A spore showing the smooth outline and triradiate mark with one forked distal end. Another spore is seen obscurely out of focus behind. × 400. V.31508.

FIG. 55. Another spore showing outline and smooth surface. × 400. On this slide entrapped among the hairs of *Anemia poolensis* is a single spore of *Lygodium poolensis*. V.31511.

FIG. 56, 57. Two similar spores. × 400. V.31508.

All the above are from Lake, Dorset (Extracted from pinnules).

FIG. 58. A spore showing obscurely the triadiate mark. × 400. V.31515. Branksome Dene, Dorset.

Anemia colwellensis n. sp.

FIG. 59. A spore somewhat collapsed showing ridged surface. × 200. V.31522.

FIG. 60. The same spore. × 400.

FIG. 61. Another spore showing the "beaded" effect where the ridges on two surfaces cross one another. × 400. V.31522.

FIG. 62. Another spore showing outline and thickness of wall. It has gaped along two rays of the triradiate mark. × 400. V.31523.

FIG. 63. Another showing a ridge branching and the rather obscure triradiate mark. × 400. V.31522.

FIG. 64. Another, side elevation, showing ridges obscurely. The spore has partly folded and collapsed. × 400. V.31523.

All the above are from Colwell Bay, Isle of Wight.

Anemia sp.

FIG. 65. Two impressions of barren pinnules. The nervation is comparable with that seen on the fertile pinnule of *A. colwellensis*. × 2. V.17498. Thorness Bay, Isle of Wight. Also figured Reid & Chandler, 1926, pl. 1, fig. 11.

Lygodium prestwichii Gardner

FIG. 66. Impression of the upper surface of a bilobed pinnule, one lobe well exposed, the other, rolled up, at *l*2. The toothed margin is seen on the left of the larger lobe. The secondary nerves. sunk in the original, appear as fine thread-like ridges, the primary nerve appears as a sharp ridge in the impression representing a sharply angled channel in the original. × 2. V.24862. Newington, Kent.

FIG. 67. The counterpart of the above showing the impression of the lower surface with conspicuous rounded midrib in the original (a rounded channel in the fossil) and the raised thread-like impressions of the sunk secondary nerves of the original. Second lobe of leaf at *l* 2. × 2.

FIG. 68. The teeth on the right margin in Fig. 67. The thread-like secondary nerves are also seen and the thickening of the margin. × 6·5.

FIG. 69. An impression of the lower surface of another pinnule with well-preserved nerves but poorly preserved margins scarcely showing the teeth. × 2. V.24859. Newington, Kent.

ANEMIA POOLENSIS, A. COLWELLENSIS, ANEMIA SP., LYGODIUM PRESTWICHI

PLATE 37

Lygodium kaulfussi Heer

FIG. 70. Impression of a barren-lobed pinnule showing nervation and entire margin. × 1·8. V.28659.

FIG. 71. Another long narrow pinnule lobe. × 1·8. V.28658.

FIG. 72. Fertile pinnule, upper surface. × 15·5. V.31524.

Fig. 73. The same, lower surface. × 15·5.

FIG. 74. Another fertile pinnule (incomplete at the base), upper surface. × 15·5. V.31525.

FIG. 75. The same, lower surface. It shows clearly the marked sinuosity of the midrib. × 15·5.

FIG. 76. A distorted fertile pinnule showing the long stalk. × 15·5. V.31526.

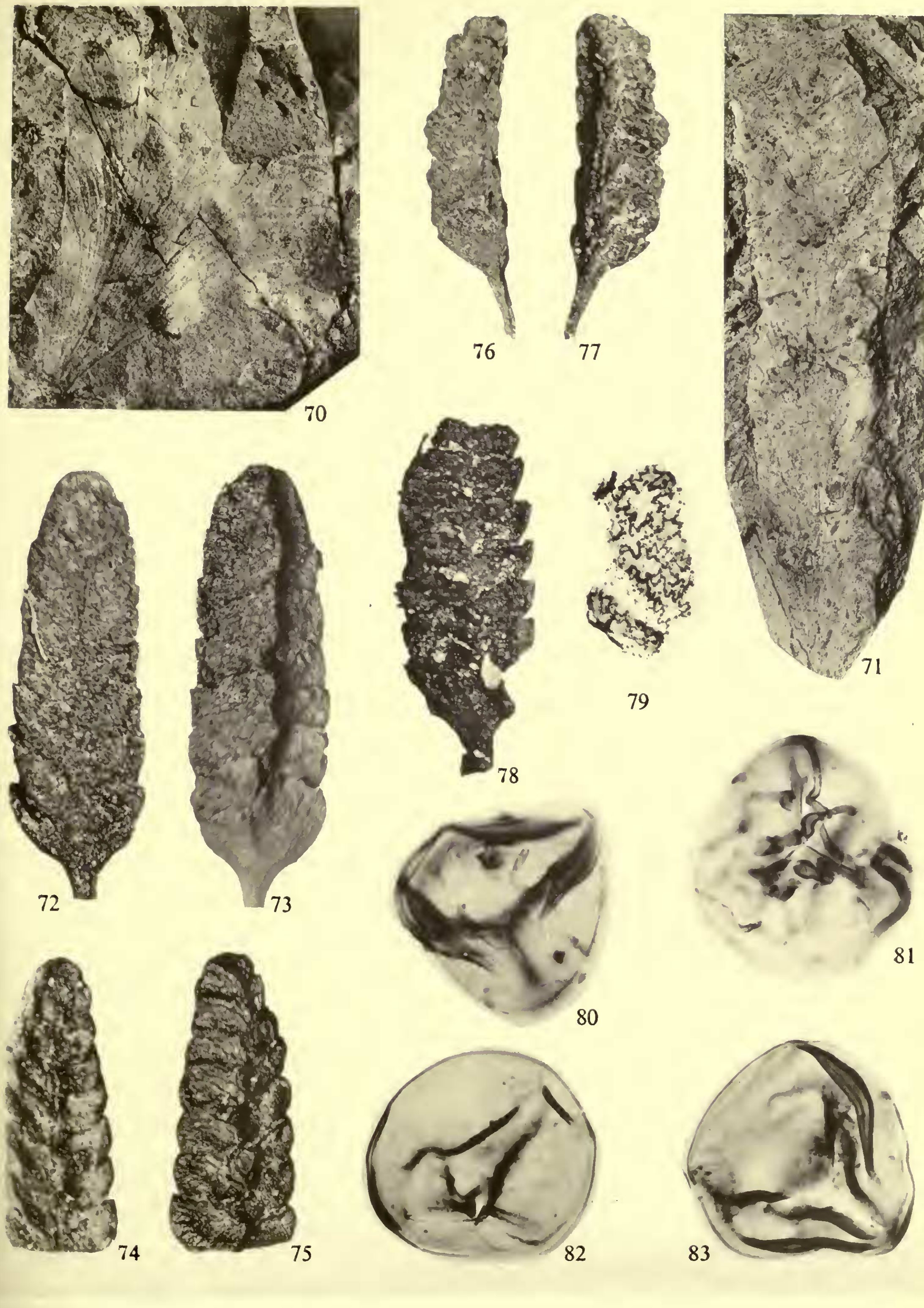
FIG. 77. The same, opposite side. × 15·5.

Fig. 78. A fertile pinnule, upper surface, somewhat battered and sand pitted. × 15·5. Specimen destroyed in macerating to release few remaining spores (slide V.31531). Branksome Dene, Dorset.

FIG. 79. Cuticle fragment from a fertile pinnule showing sinuous cells and " beaded " thickening, giving a " dotted " effect. × 150. V.31527.

FIGS. 80–83. Typical spores extracted from two fertile pinnules, showing the smooth surface and triradiate mark. Folds shown are due to partial collapse. × 400. Figs. 80, 81 are from V.31528. Figs. 82, 83 are from V.31529.

All the above, except Fig. 78, are from Studland, Dorset.



LYGODIUM KAULFUSSI

PLATE 38

Lygodium kaulfussi Heer

FIG. 84. An unusually large and thick-walled spore extracted from one of the fertile pinnules. It has burst along the triradiate mark. × 400. V.31530. From the pinnule which yielded the spores figured in Pl. 37, figs. 82, 83 (V.31529).

FIG. 85. A typical spore showing the smooth surface and triradiate mark. Folds are due to collapse. × 400. V.31528. The spores in Pl. 37, figs. 80, 81 are from the same pinnule.

Both the above are from Studland, Dorset

FIG. 86. A large spore removed from the fertile pinnule (Pl. 37, fig. 78) showing the smooth surface and triradiate mark and small fork at the termination of the ray at the top of the figure. × 400. V.31531. Branksome Dene, Dorset.

FIG. 87. A collapsed isolated spore apparently of this species. × 400. V.31532. Cliff End, nr. Mudeford, Hampshire.

Lygodium poolensis n. sp.

FIG. 88. A naturally macerated fragment of fertile pinnule showing the recurved sporangia exposed by the decay of the enveloping pinnule segments and bracts. Only one (x) is complete. This one shows the annulus by reflected light. *r*, *r* remains of other sporangia. × 50. V.31533. Holotype.

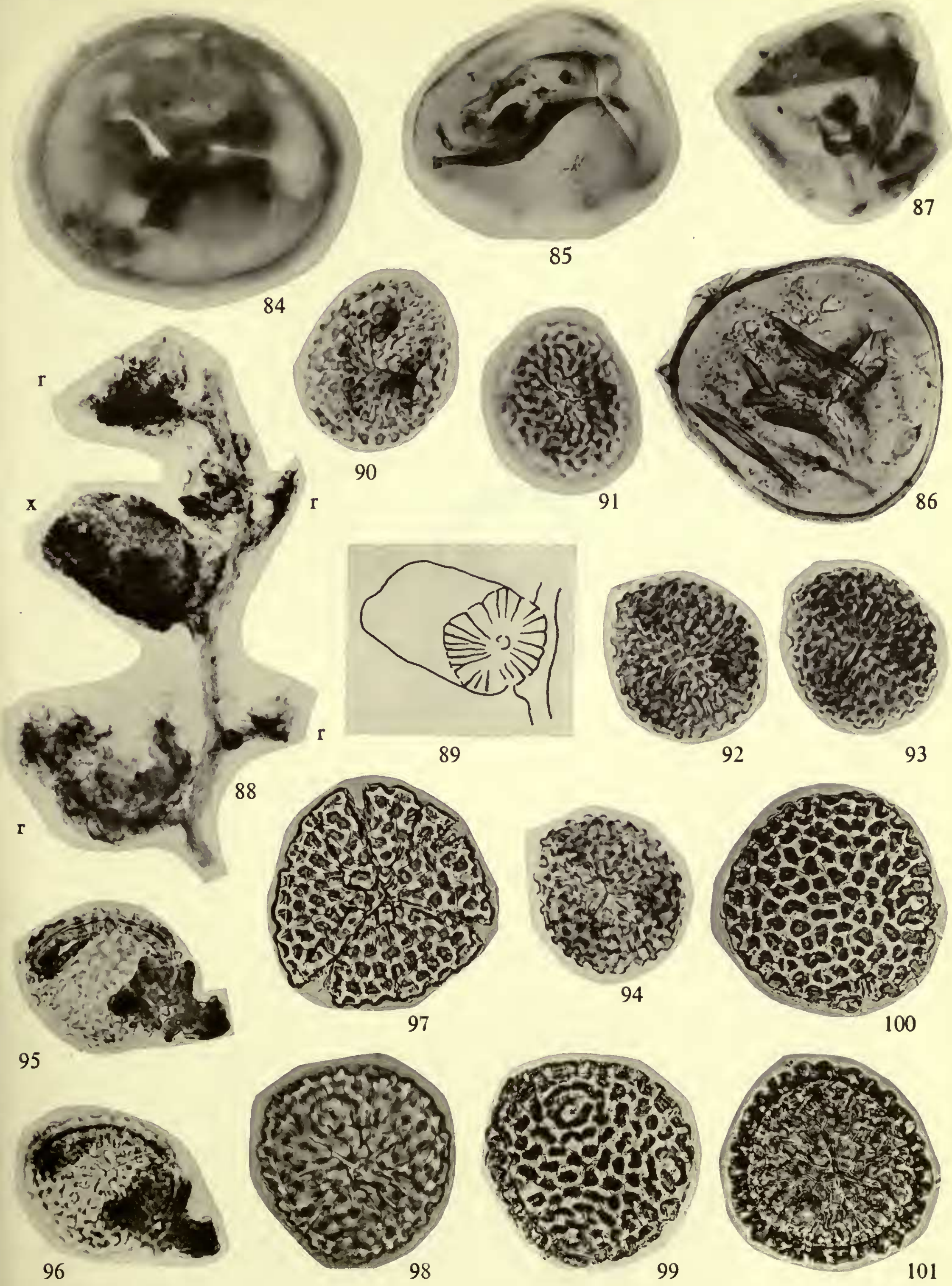
FIG. 89. Diagram of the sporangium (*x*) in Fig. 88 to show the position of the annulus which is very obscurely seen in the photograph.

FIGS. 90–96. Four spores from the above fertile pinnule. They show the deeply pitted surface (the pits bounded by the walls of confluent tubercles?). Figs. 95, 96 represent the same crushed spore. Fig. 95 is focused to show the thickness of the wall, Fig. 96 the extent of the triradiate mark. Figs. 90, 91 and 94 also show the triradiate mark. Figs. 92–94 represent the same spore differently focused to show triradiate mark, outline and surface ornamentation. Pits show best in Fig. 93, tubercles forming the walls of pits in Fig. 92 (top right). All × 400. V.31534–36.

All the above are from Lake, Dorset.

Lygodium scandens Sw. (Recent)

FIGS. 97–101. Spores. Fig. 97 shows a crushed spore which has split along the triradiate mark. Fig. 98, the triradiate mark in an uncrushed spore. Fig. 99 is the same as Fig. 98 but the focus shows the wall thickness and pitted surface. Fig. 100, another spore showing surface structure and pitting. Fig. 101, another focused to show wall thickness in optical section. It also shows obscurely the triradiate mark. Figs. 97, 99–101. × 400. V.31537. Fig. 98. × 400 approx. Recent (Ross 123. Nigeria).



LYGODIUM KAULFUSSI, L. POOLENSIS, L. SCANDENS (Recent)